

A CASE OF PHORESIS OF SPHAERIIDS BY CORIXIDS: FIRST REPORT FOR THE AMERICAS

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INTRODUCTION

Dispersal represents a key process in determining the genetic structure and demography of populations. This process reduces competition among siblings, reduces competition between parents and offspring, reduces the likelihood of inbreeding, increases recolonization following local extinctions, also decreasing the risk of local extinction (Pechenik, 1999). Similarly, the modes of reproduction and dispersal can play a major role in species longevity, geographic distribution, and rate of speciation (Mayr, 1970; Stanley, 1979).

In freshwater bivalves, a free-living larval stage is frequently suppressed; consequently, the dispersal of a species relies on the capacities of juvenile and adult stages. Dispersal mechanisms include rafting (i.e., the transport of an organism on a drifting object); current-mediated dispersal of juveniles suspended in water (McKillop & Harrison, 1982); airborne dispersal (anemochory) of juveniles and adults (e.g., hurricanes, tornadoes, and other twist-ers) (Rees, 1965, and references therein); and dispersal by biotic (either natural or anthropogenic) vectors, with vertebrates or invertebrates acting as carriers (Kappes & Haase, 2012, and references therein).

Darwin (1882) was the first to assess the evolutionary importance of the long-distance transportation of freshwater molluscs by insects. The present paper provides the first record on the occurrence of this phenomenon in the Americas.

MATERIAL AND METHODS

Bivalves associated to insects were found in a small (550 m²) artificial reservoir located at 16°59'33.43"S, 68°04'30.83"W, approximately 90 km southeast of Lake Titicaca Menor (or Lake Huiñaimarca), Bolivia, at 3,993 m altitude.

This temporary water body was very shallow (< 0.6 m), turbid (clayey), with sandy-muddy bottom, devoid of aquatic vegetation, and used as a cattle drinking trough (Fig. 1).

The climate of this region is characterized by reduced atmospheric humidity, high levels of UV radiation, low temperatures (extreme daily temperatures ranging from -10 to 21°C), marked daily fluctuations of temperature (up to 25°C) due strong solar radiation and intense irradiative cooling by night. Scarce rainfalls (< 300 mm/year) are concentrated during the austral summer.

Qualitative invertebrate samples were taken with a hand net (320 µm mesh). Since the sampling method was not intended for infaunal organisms, molluscs were collected unexpectedly because of their attachment to nectonic organisms. Samples were preserved in situ in ethanol. All the specimens were measured with a precision of 0.025 mm with a Leica M80 stereoscopic microscope. A preliminar identification of bivalves was made based on shell morphology. In the absence of adult specimens, their identity was confirmed by Dr. Taehwan Lee, by using molecular information from 16S, COI and ITS1 gene sequences. Voucher specimens were deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In 38868), Argentina and in the University of Michigan, USA.

RESULTS

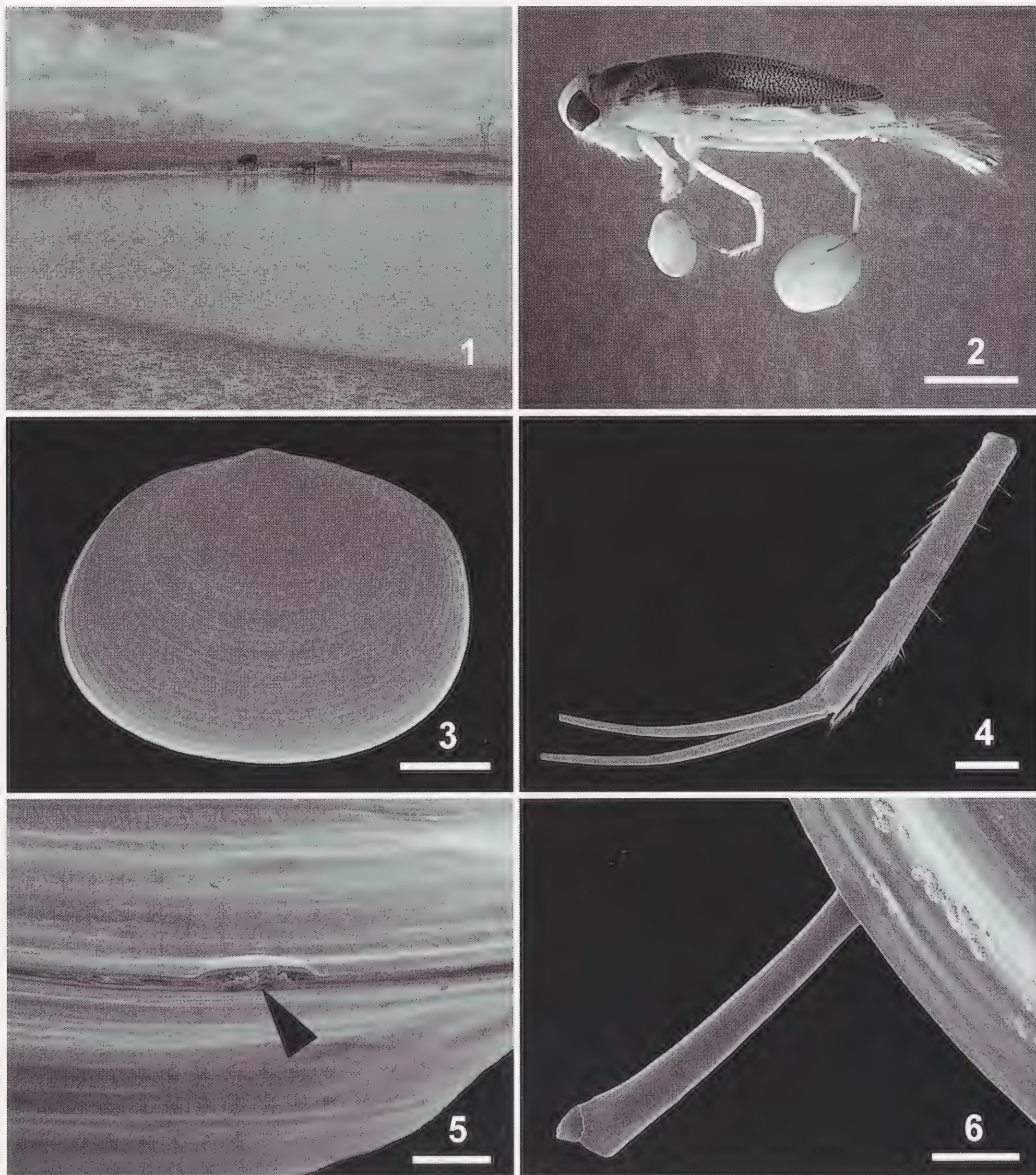
Thirty-four juvenile (1.50–2.45 mm length) fingernail clams were collected. The shell shape of the examined juvenile specimens (Fig. 3) agrees with the description provided by Kuiper & Hinz (1984) for *Sphaerium* (*Musculium*) *auricochae* (Philippi, 1869) (Veneroida: Sphaeriidae).

Seven specimens of *Ectemnostega* (*Ectemnostegella*) *quechua* Bachmann, 1961

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FIGS. 1–6. Phoresis of sphaeriids by corixids. FIG. 1: Collecting site; FIG. 2: *Ectemnostega quechua* carrying two juveniles of *Sphaerium lauricochae* clipped to the tarsal claws of its middle legs. Scale bar = 2 mm; FIG. 3: Outer left view of a juvenile specimen of *S. lauricochae*. Scale bar = 500 μ m; FIG. 4: Tips of the tarsal claws of a middle leg of *E. quechua* damaged by the attachment and detachment of a juvenile of *S. lauricochae*; FIG. 5: Ventral view of a juvenile of *S. lauricochae*. The arrow shows the injury produced in the shell margin after the attachment to a corixid claw. Scale bar = 100 μ m; FIG. 6: Lateral view of a juvenile of *S. lauricochae* with a claw fragment trapped within the valves. Scale bar = 100 μ m.

(Heteropta: Corixidae) were found carrying fingernail clams (Fig. 2). From them, 6 were adult specimens, both brachypterous (male: 7.1 mm long; females: 7.2, 7.3, 7.5 mm long) and macropterous (females: 7.9, 8.3 mm long), and a nymph of the 5th instar (5.6 mm long).

The phoretic relationship of *S. lauricochae* with *E. quechua* was verified in only one out of 42 water bodies surveyed. In all cases, the clams were clipped either to one or both tarsal claws of the middle legs. Usually a single bivalve per corixid was found, except for one that carried two of them (Fig. 2). In the latter case, one bivalve on each side of the insect was found (Fig. 2). The tight attachment of fingernail clams to corixids damage both the shell margin (it may show an indentation or a claw fragment within shell: Figs. 5, 6) and the insect claws (they present trimmed tips: Fig. 4). Therefore, direct and indirect evidences show that at least 44% of the clams collected in the finding place were involved in the association. The attachment to insects occurs over the whole size range of the studied bivalves.

DISCUSSION

Sphaeriids are brooding bivalves that retain their embryos in marsupial pouches derived from parental gills (Heard, 1977). Known dispersal mechanisms of Sphaeriidae include longitudinal movements in flowing waters, and lateral movements among unconnected habitats by biotic and abiotic vectors. In this regard, fishes and birds have been reported as carriers of sphaeriids that, after being ingested, can survive gut passage (Brown, 2007); other animals have been reported carrying sphaeriids attached to their body (Mackie, 1979). The latter condition is known for bivalves clamped onto ducks (Green & Figuerola, 2005), salamanders (Davis & Gilhen, 1982; Wood et al., 2008), frogs (Gutleb et al., 2000), and insects (Rees, 1965; Mackie, 1979). Except for some reports on bivalves clipped to Odonata and Coleoptera (Kew, 1893), most of them involve hemipterans of the genera *Nepa*, *Notonecta*, *Corixa*, and *Sigara* (Kew, 1893; Cash, 1912; Griffith, 1945; Fernando, 1954; Lansbury, 1955; Soldán et al., 1989). Furthermore, except for the report by Griffith (1945) on "small clams" carried by nymphs of Corixidae, all other references involve adult insects as carriers.

The present study provides the first record for the Americas of fingernail clams transported by insects. The sphaeriid *Sphaerium lauricochae* has been reported from lentic and lotic freshwater habitats of the Altiplano of Bolivia, Chile, Peru, and northwestern Argentina (Kuiper & Hinz, 1984; Ituarte, 2005; Parada & Peredo, 2006). On the other hand, the heteropteran *Ectemnostega quechua*, reported from Peru, Bolivia and northwestern Argentina, from Jujuy to Catamarca provinces (Morrone et al., 2004), is a characteristic inhabitant of small water bodies, either shallow or very shallow, with scarce or no vegetation, and variable temperatures (Bachmann, 1981).

The studied bivalves were nipped on adult males and females, either brachypterous or macropterous, as well as nymphs. In all cases, the sphaeriids were nipped on the tip of the middle legs of the corixids that bear two long and slender tarsal claws that are used by the insects to hold themselves to the bottom of the waterbody while resting (Fernando, 1954; Bachmann, 1981).

As it was reported by Darwin (1882), Standen (1885), Kew (1888, 1893), and Lansbury (1955) for the hemipterans *Nepa* and *Corixa punctata*, most of the *Ectemnostega* specimens here studied carried a single fingernail clam. On the other hand, Kew (1893) and Cash (1912) found some specimens of *Nepa* and *Corixa* carrying two bivalves, as herein reported. Kew (1893) even reported up to three bivalves clipped to a British corixid.

Darwin (1882), Green & Figuerola (2005) and Wood et al. (2008) reported that the attachment by bivalves usually damages the toes of amphibians and birds, or the legs of insects. This kind of damage was also observed in the case of *E. quechua*, whose middle leg tarsal claws appear broken at the tip. On the other hand, fingernail clams close their valves so tightly on the claws of corixids that their shell margins are injured (Fig. 5). This injury in the bivalve shell has not been previously reported.

The extensive list of aquatic insects reported as bearing sphaeriids nipped on their bodies reveals the potential of this relationship for bivalve dispersal. In this sense, it should be noted the great mobility usually exhibited by heteropterans. *Corixa punctata* and *Sigara lateralis*, for example, are known to have high migration rates (Brown, 1951; Fernando, 1954). Popham (1952) estimated that *Sigara striata*, *S. germari* and *S. nigrolineata* could migrate

about 10–13 km on a windless day, and *Corixa punctata* may have an even greater range. Unfortunately, nothing is known about the mobility of *E. quechua*. Some species, such as *Sphaerium corneum* (Linnaeus) may remain attached for up to six days on the legs of the coleopteran *Dytiscus marginalis* (Linnaeus) (Darwin, 1882). The great mobility and gregarious habits of corixids, and the long time of attachment reported for some sphaeriids to insects, pleads for them as suitable dispersal agents. The occurrence of closely located ponds could favour a stepping stone colonization. Since corixids abandon their habitats when they dry up, or when temperatures get too high, or for dispersal purposes, mainly during the night (Bachmann, 1981), such behaviours may also favour bivalve survival during transport. The finding of bivalves clipped to non-flying corixids (nymphs and brachypterous adults) suggests that this relationship does not necessarily imply the dispersal between different aquatic habitats (lateral dispersal), but their relocation to deeper waters within the same waterbody, when the habitat starts to dry. Corixids are fast swimmers that move regularly from the bottom to the surface to renew the atmospheric air reserve (plastron) that they carry below the hemelytra (Bachmann, 1981). Therefore, in situ movements of corixids could favour sphaeriids at finding more suitable microhabitats. It cannot be dismissed that shell closing and clamping of *S. lauricochae* is automatically triggered by any moving object (small or large, live or inert) that touches the bivalve. Although not always successful in securing long distance dispersal, such an evolutionary fixed response would still be adaptive for sphaeriid survival.

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